


New data about semicircular canal morphology and locomotion in modern hominoids

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Abstract

The labyrinth has two functional parts: the cochlea for audition and the vestibular system for equilibrioception. In the latter, the semicircular ducts and the otolithic organs are sensitive to rotational and linear accelerations of the head, respectively. The labyrinthine morphology influences perception accuracy, hence the adaptation to a specific locomotor pattern. The aim of this study is to determine the relationship between locomotion and semicircular canal morphology using geometric morphometrics, and to explain these links with existing functional models. The influence of factors other than functional constraints on labyrinthine morphology is discussed. The left bony labyrinth of 65 specimens was extracted virtually. Five extant hominoid species with various locomotion modes were sampled. A set of 13 landmarks was placed on the semicircular canals. After a Procrustes fit, their coordinates were analyzed using a principal component analysis. It was found that labyrinthine morphology is significantly distinct between species. More specifically, the differences involve a posterolateral projection of the lateral semicircular canal and the rotation of this canal relative to the vertical canals. This rotation occurs in the sagittal plane, which is consistent with previous studies based on traditional morphometrics. Among extant hominoids, the shape of the canals potentially discriminates species based on posture. This result could be used to reconstruct the locomotor pattern of fossil hominoids.

Key words: bony labyrinth; geometric morphometrics; hominoidea; inner ear; locomotion.

Introduction

Among all the extant primates, *Homo sapiens* is the only species exclusively using bipedal locomotion. Many primates use terrestrial bipedalism, but the form practiced by humans is specific: they walk with straight hips and knees (Schmidt, 2010). This specificity is enabled by morphological adaptations, which are major criteria in palaeoanthropology to determine if a fossil species belongs to the human branch.

Primates show a large range of locomotor behaviors in both arboreal and terrestrial environments. These can be

classified into five categories: bipedalism; quadrupedalism; quadrumanous climbing and scrambling; leaping and diving; and suspension (Susman et al. 1980; Fleagle, 1999; Schmidt, 2010). The locomotor behavior of a species depends on its activity: travel, foraging or escape (Schmidt, 2010). Among primates, Hylobatidae, especially the smaller ones, are the most specialized brachiators (Tuttle, 1969; Fleagle, 1999; Schmidt, 2010). Their morphology is adapted to this mode of locomotion: long arms compared with their bodies and wrist joints allowing 180° of rotation. They also use vertical climbing and bipedal arboreal walking. The predominant locomotor modes of the great apes are climbing, quadrupedal walking and arm swinging (Tuttle, 1969; Fleagle, 1999; Schmidt, 2010). They have very mobile limbs and long arms. Orangutans are the most arboreal of the great apes, whereas gorillas are the least. In trees, orangutans use cautious climbing and clambering, a form of suspension with the contribution of the hindlimbs to support the body mass, while gorillas only climb and chimpanzees prefer quadrumanous walking and climbing. On the ground, the great apes use quadrupedalism: fist walking for orangutans and two different forms of knuckle-walking for gorillas and chimpanzees (Kivell & Schmitt, 2009). Apes occasionally use

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bipedalism (Schmidt, 2010). Gibbons walk bipedally in the trees and on the ground, often with their arms raised above their head. Chimpanzees and bonobos walk bipedally on the ground, with bent hips and knees.

Reconstructing the locomotor behavior of fossil species is difficult because post-cranial remains and footprints are rare. That is, using the bony labyrinth has been suggested as an indirect way to infer the locomotion of fossil species (Spoor et al. 1994; Spoor, 2003). Indeed, the labyrinth or inner ear participates in two sensory functionalities: audition and equilibrioception. More precisely, the cochlea detects sounds whereas the otolithic organs and the semicircular ducts are sensitive to linear and circular head movements, respectively (Sakka & Vitte, 2004; Graf & Klam, 2006). The inner ear is filled with a fluid called endolymph. In the ampulla of each semicircular duct, hair cells are attached to a gelatinous mass: the cupula. When the head moves, so does the endolymph in the membranous labyrinth. This movement is detected by the hair cells.

Biophysical models were built to understand the dynamics in a semicircular duct (Steinhausen, 1933; Van Egmond et al. 1949; Jones & Spells, 1963). The duct dimensions (arc size R , radius r of the cross-sectional area) are a compromise between three parameters (Muller, 1999): the response time for a maximum endolymph displacement (short time constant T_2); the maximum endolymph displacement after a stimulus (x_{\max}); and the Reynolds number (Re). Indeed, an efficient rotation sensor needs a high response speed (low T_2), a high sensitivity (high x_{\max}) and an undisturbed laminar endolymph flow ($Re < 50$). Equations show proportionality between T_2 and r^2 , x_{\max} and $R \times r^2$, Re and $R \times r$. For a constant perimeter, sensitivity decreases when the canal is not circular (McVean, 1999). However, this decrease is insignificant compared with the role of the cross-sectional area, except for a very strong eccentricity. The interconnection between the semicircular ducts influences the sensitivity of the system. When the ducts are not orthogonal, the performances of the system can be improved by amplification or compensation of the neural impulses in the different ducts (Muller & Verhagen, 1988). Furthermore, the anterior and posterior semicircular ducts share a branch, the common crus, and so they are mechanically coupled (Muller & Verhagen, 2002a,b,c). Consequently, the sensitivity of the system is increased for pitch head movements when these canals form an obtuse angle or when their dimensions are different (arc size, cross-sectional area or eccentricity).

Because the biomechanical properties of the semicircular ducts influence the detection of head movement, we propose three hypotheses to be tested about a link between their morphology and locomotion.

1 The orthograde posture is less stable than the pronograde posture for two reasons. Firstly, the body mass is generally supported by two limbs instead of four, at least in terrestrial bipedalism. Secondly, the head is higher relative to the body's center of gravity. This leads

to a larger amplitude in the head movements. Therefore, species using an orthograde posture need a less sensitive vestibular system to avoid overstimulation, but with a shorter response time for a better stabilization. The anterior and posterior semicircular canals (ASC and PSC) are more likely to show these features than the lateral one, as rotations in the vertical plane control balance, whereas rotations in the horizontal plane control navigation (Fitzpatrick et al. 2006).

2 Whereas arboreal species move in a three-dimensional environment, terrestrial species use only two dimensions for their locomotion. So it is possible to hypothesize that the selective pressure for a good sensitivity in the vertical direction is weaker when it comes to terrestrial species, in contrast to arboreal species. For terrestrial species, the result could be either a higher intraspecific variability of the vertical semicircular ducts, or different mechanical properties between the horizontal and the vertical ducts.

3 The more agile species make fast and large head movements. They need a short response time, but duct sensitivity must be limited to avoid overstimulation (Spoor & Zonneveld, 1998). Conversely, the slower species need a better sensitivity, but their response time can be longer. For these species, the functional constraints could be weaker (Perier et al. 2016).

In mammals, the osseous and membranous semicircular canals have similar orientations and can therefore be used indifferently to study labyrinth geometry (Ifediba et al. 2007). The labyrinths in both sides are symmetrical vis-à-vis the midsagittal plane and the three canals of each labyrinth are roughly orthogonal, allowing the detection of head rotations in all directions (Graf & Klam, 2006). Each semicircular canal is approximately coplanar to the corresponding extraocular muscle, allowing the gaze to be maintained during locomotion (Ezure & Graf, 1984). Yet there is significant variation from alignment between these two planes, linked to changes of orbit morphology (Jeffery & Cox, 2010). The lateral semicircular canal (LSC) is tilted back by 20–25° in relation to the Frankfurt horizontal plane, which is roughly parallel to the Earth horizontal when the head is in a rest position (Graf et al. 1995). The vertical canals form angles of about 45° relative to the midsagittal plane of the head, and every ASC is roughly coplanar with the contralateral PSC, allowing them to operate as a push–pull pair: during a rotation, one canal is excited while the other one is inhibited (Graf & Klam, 2006). These orientations are maintained in all the mammal species with little variability, even for species with radically different basicranial architectures, labyrinth morphologies and optic axis orientation, suggesting a strong functional significance, and therefore a strong selective pressure (Spoor & Zonneveld, 1998). However, there are slight but significant differences in orthogonality, symmetry and coplanarity (Berlin et al. 2013).

Linear relationships exist among the cross-sectional radii of the semicircular ducts, among their arc sizes, and between the arc size and the cross-sectional radius of each duct (Muller, 1990, 1999). A membranous duct is generally very close to the outer wall of the osseous canal by which it is enclosed, and so their arc sizes are similar. However, the cross-sectional areas of the membranous duct and the osseous canal are different, especially in humans where the ratio of duct to canal cross-sectional areas is lower than 10% (Curthoys et al. 1977a,b). Whereas there is a negative allometric increase of canal dimensions with the body mass (Jones & Spells, 1963), the body mass is not correlated with the deviation from planarity or circularity (Cox & Jeffery, 2010). The semicircular arc size also increases with eye size and visual acuity, independently from body mass and phylogeny (Kemp & Kirk, 2014).

The semicircular canal morphology (distances, angles) is related to locomotor behavior. Aquatic mammals can be discriminated from terrestrial ones by the elliptic shape of the ASC (Georgi, 2008; Ekdale, 2016) and the reduced size of the vestibular system (Ekdale, 2013). In the squirrel-related clade, the morphology of the labyrinth discriminates the fossorial species from the gliding and flying ones (Pfaff et al. 2015). For the non-avian dinosaurs, the area surrounded by the ASC is large in bipedal species in comparison to the quadrupedal ones (Georgi et al. 2013). Among primates, the obligatory bipedalism in *H. sapiens* and *H. erectus* was linked to large vertical semicircular canals and a small LSC, relative to the body mass (Spoor et al. 1994, 1996; Spoor & Zonneveld, 1998). It was also proved that the semicircular canal radii, again relative to the body mass, increase with agility (Spoor et al. 2007). This relationship was used to infer the locomotor behavior of fossil species in diverse groups: early primates (Silcox et al. 2009), early strepsirrhine primates (Walker et al. 2008) and anthropoids (Ryan et al. 2012).

The bony labyrinth morphology reflects not only locomotor behavior, but also a phylogenetic heritage. For several mammalian groups, phylogenetically informative features can be found in the bony labyrinth (Ekdale, 2013; Billet et al. 2015; Ekdale, 2016). Therefore, linear and angular measurements were also used to specify the phylogenetic position of species with unclear affinities, such as *Oreopithecus bambolii* (Rook et al. 2004), or to attribute isolated temporal bones to a species (Spoor, 1993; Braga et al. 2013).

However, traditional morphometrics (Spoor & Zonneveld, 1995) only offer a partial description of the labyrinthine shape, especially the canal torsion and lengthening direction. Geometric morphometrics, which take into account these parameters, allow the detection of significant differences even among very similar species (Gunz et al. 2012). Therefore, this method was used to specify the phylogeny of early Strepsirrhini (Lebrun et al. 2010) and of Adapiiformes (Lebrun et al. 2012).

Those observations lead to the following questions. (i) Can 3D geometric morphometrics highlight a link between the morphology of the semicircular canals and locomotion in Hominoidea? (ii) If this link exists, what functional processes induced by the morphology allow a better adaptation to the locomotor behavior? (iii) Does the labyrinthine morphology only depend on functional constraints in hominoids?

Here, the semicircular canal shapes among five extant hominoid species are compared using a geometric morphometric method: *Hylobates lar carpenteri*, *Pongo pygmaeus*, *Gorilla gorilla*, *Pan troglodytes* and *H. sapiens*. As the species are closely related, it can be hypothesized that morphology does not depend on phylogeny within this group. The aim is to determine the labyrinthine morphology corresponding to each locomotor behavior. This study on extant species could provide a framework to infer the locomotor behavior of extinct hominoid species, especially the evolution of bipedalism in the human branch.

In this article, the term Hominoidea corresponds to the great apes and humans (extant genus *Pongo*, *Gorilla*, *Pan* and *Homo*), and it is the sister family of Hylobatidae (lesser apes) in the superfamily Hominoidea (Delson et al. 2000).

Materials and methods

Materials

Ethics statement

The human and non-human samples (Table S1) were composed exclusively of dry skulls donated and curated in institutions from which permissions were obtained to access the specimens. Data reported here involved only the processing of micro-computer tomography (CT) scans, without any experimentation on subjects. That is why no permits were required for the described study. The human skeletal sample is curated by the Centre de Valorisation des Collections Universitaires (CVCU) of the Université de Poitiers (France) and housed in the Musée Sainte-Croix (Poitiers, France). The ape skeletal sample is curated by the Anthropologisches Institut und Museum (Zurich, Switzerland) and the Université de Poitiers (France). The collections were made in the late 19th–early 20th centuries and donated to these institutions (by G. Vacher de Lapouge for the human specimens), where they are publicly accessible.

Sample composition

The sample consisted of 65 extant hominoid skulls (Table 1; details in Table S1), including 10 Carpenter's lar gibbons (*H. lar carpenteri*), 10 orangutans (*P. pygmaeus*), 15 gorillas (*G. gorilla*), 12 chimpanzees (*P. troglodytes*) and 18 humans (*H. sapiens*). Among the chimpanzees, at least one specimen belongs to the subspecies *P. t. verus* and seven specimens to *P. t. troglodytes*. Among the gorillas, all the specimens of the collections of the Anthropologisches Institut und Museum, Zurich belong to the subspecies *G. g. gorilla*. Among the orangutans, at least two specimens belong to the subspecies *P. p. abelii* and two specimens to *P. p. pygmaeus*. Subspecies are undetermined for the other specimens. All specimens are adults (M3 fully erupted), except for one chimpanzee, three gorillas and one orangutan. The maturity of these individuals

Table 1 Sample composition.

Species	Males	Females	Uncertain	Total
<i>Homo sapiens</i>	7	9	2	18
<i>Pan troglodytes</i>	6	5	1	12
<i>Gorilla gorilla</i>	7	7	1	15
<i>Pongo pygmaeus</i>	5	5	0	10
<i>Hylobates lar carpenteri</i>	5	5	0	10
Total	28	29	4	65

should not affect the morphology. Indeed, there is evidence in humans that bony labyrinth size and shape changes only occur during the prenatal stages (Jeffery & Spoor, 2004; Mejdoubi, 2015). Males and females are roughly in equal number for each species. Humans are European (France, Germany) and African (Benin, Gabon and Algeria).

Specimen acquisition

The temporal area of the specimens from the IPHEP collections was scanned there using a microtomograph Xcom, with isometric voxel sizes between 45 and 65 μm (Table S1). For the specimens from the AIM collections, the scan of the whole basicranium was performed by one of the team members (P.S.) on the micro-CT system built at the Eidgenössische Materialprüfungs- und Forschungsanstalt, Dübendorf, Switzerland, with isometric voxel sizes between 69 μm for gibbons and 156 μm for gorillas (Table S1).

Data processing

The left bony labyrinth of each specimen was extracted virtually from the CT-scans using *AVIZO* software (Visualization Sciences Group). The centerline of the 3D volume was calculated using the *AutoSkeleton* module (coefficients: smooth = 0.5; attach to the data = 0.25; number of iterations = 10), and the computation errors such as duplicated edges or extra edges between two lines were corrected using the *LineSet* editor module.

Data analysis

As the cranial anatomical planes cannot be defined on the CT-scans of the temporal bone, approximations of these planes are locally defined. In this study, the planar orientation of the LSC corresponds to the transverse plane. The sagittal plane is defined as the plane

bisecting the angle opening anteroposteriorly between the planar orientations of the two vertical semicircular canals (ASC and PSC). The coronal plane corresponds to the plane orthogonal to both the sagittal and transverse planes. Three axes are defined that correspond to the cranial anatomical directions: superior-to-inferior; anteromedial-to-posterolateral; and anterolateral-to-posteromedial lines (Fig. 1).

For the analysis of the bony labyrinth morphology, 13 landmarks (Fig. 1; Table 2) were positioned using *AVIZO* software (Visualization Sciences Group). They correspond to the landmarks located on the common crus and the semicircular canals defined by Lebrun et al. (2010). Landmark 1 corresponds to the bifurcation of the common crus. Landmarks 2, 6 and 10 are the centers of the ampulla of each semicircular canal. The locations of the other landmarks are in accordance with the three axes defined above.

The 3D landmark configurations were superimposed by a Procrustes superimposition (Rohlf & Slice, 1990; Bookstein, 1991) using *MORPHOJ* v1.0e software (Klingenberg, 2011). It included scaling, translation and rotation. During this process, the centroid size of each configuration is computed. The centroid size of a set of landmarks is defined as the mean squared distance of the landmarks from their common centroid (Bookstein, 1991). A multivariate regression was performed between the landmark Procrustes coordinates (dependent variables) and the natural logarithm of the centroid size (independent variable) to detect the allometric effects. A permutation test was performed with 10 000 iterations against the null hypothesis of independence between the size and shape variables (Klingenberg, 2011). A principal component analysis (PCA) was realized to study shape variation (Zelditch et al. 2004; O'Higgins & Jones, 2006). The regression residuals of the multivariate regression were used for the PCA in order to correct the effects of allometry rather than for the landmark Procrustes coordinates. Both analyses were conducted using *MORPHOJ* v1.0e software (Klingenberg, 2011). The 3D shape changes associated to the principal components (PCs) and to the regression score (Drake & Klingenberg, 2008) were visualized using *R* v3.0.2 software (R Development Core Team, 2008).

Using *R* v3.0.2 software (R Development Core Team, 2008), diverse analyses of variance (ANOVA) were performed to study the interspecific and intraspecific variabilities. Size differences between sexes and among taxa were tested by ANOVAs of the labyrinth centroid size. The shape variability was tested by multivariate analyses of variance (MANOVAs) of the significant PCs. These analyses were followed by Tukey's honest significant difference (HSD) *post hoc* tests, which are very conservative, to assess the pairwise differences among species and the sexual dimorphism in one species. Specimens of uncertain sex are excluded from the analyses of variance when sexual

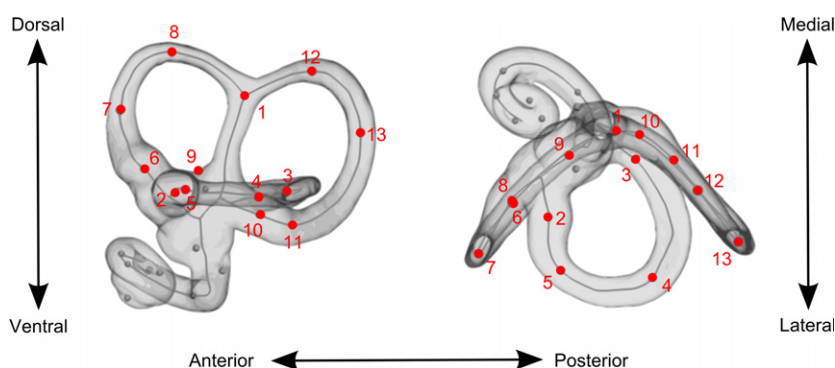


Fig. 1 Landmarks used for the geometric morphometric analysis of the left bony labyrinth (modified after Lebrun et al. 2010). Specimen: *Pongo pygmaeus* 1988, lateral (left) and superior (right) views. Landmark 9 was located on the surface of the bony labyrinth. All the other landmarks were located on the center of the lumen of the semicircular canals, defined by skeletonization (grey line) (see Table 2 for the landmark definitions).

Table 2 Landmarks definitions, adapted from Lebrun et al. (2010).

Number	Name	Definition
1	Crus commune apex	Bifurcation point of the common crus
2	Canalis lateralis ampulla	Center of the ampulla of the LSC
3	Canalis lateralis posteromedial	Posteromedial-most point of the LSC
4	Canalis lateralis posterolateral	Posterolateral-most point of the LSC
5	Canalis lateralis anterolateral	Anterolateral-most point of the LSC
6	Canalis anterior ampulla	Center of the ampulla of the ASC
7	Canalis anterior anterolateral	Anterolateral-most point of the ASC
8	Canalis anterior superior	Superior-most point of the ASC
9	Canalis anterior inferior	Inferior-most point of the ASC
10	Canalis posterior ampulla	Center of the ampulla of the PSC
11	Canalis posterior inferior	Inferior-most point of the PSC
12	Canalis posterior superior	Superior-most point of the PSC
13	Canalis posterior posterolateral	Posterolateral-most point of the PSC

ASC, anterior semicircular canal; LSC, lateral semicircular canal; PSC, posterior semicircular canal.

dimorphism is tested. For sexual dimorphism, the results of each ANOVA correspond to the differences between sexes, meaning the difference between the males of all species and the females of all species, and the sex–species interactions, i.e. the difference among all possible species/sex combinations. The tests are considered significant when $P < 5\%$, with a null hypothesis of no difference between the tested groups. For each taxa, the distribution of the shape is estimated using the 68.2% confidence interval, defined as the sample mean \pm the sample standard deviation.

In order to evaluate the phylogenetic signal in the morphology of the semicircular canals, the shape was mapped onto the phylogenetic tree using MORPHOJ v1.0e software (Klingenberg, 2011). The PC scores were used as phenotypic data. The phylogenetic tree was a phylogram extracted from the GenBank taxonomy for the following species: *H. sapiens*, *P. t. troglodytes*, *G. g. gorilla*, *P. pygmaeus*, *H. lar carpenteri* (File S1). The data were available on the 10kTrees website, version 3 (Arnold et al. 2010). The method used for the mapping was squared-change parsimony, weighted by the branch lengths in the tree (considered rooted). Performed permutation tests were also performed with 10 000 iterations against the null hypothesis of a complete absence of phylogenetic signal in the phenotypic data (Klingenberg & Gidaszewski, 2010). One test was conducted for each type of phenotypic data: centroid sizes, Procrustes coordinates and PC scores.

Three aspects of locomotion were tested: agility, substrate and posture. For each aspect, three locomotor categories were defined and every species was included in one category, based on its behavior. For locomotor agility, *H. lar carpenteri* is considered as 'fast', *G. gorilla* and *P. pygmaeus* as 'slow', and the two other species as 'medium' (Ryan et al. 2012). Regarding the substrate, *G. gorilla* and *H. sapiens* are mostly terrestrial, whereas *H. lar carpenteri* is mostly arboreal, and *P. troglodytes* and *P. pygmaeus* can be considered as 'semi-terrestrial' (Fleagle, 1999; Schmidt, 2010). *Gorilla gorilla* is mostly pronograde, *P. troglodytes* uses both pronograde and orthograde postures, and the other hominoids are mostly orthograde. For each aspect of locomotion, a canonical variate analysis (CVA) was conducted using MORPHOJ v1.0e software (Klingenberg, 2011). The aim of this analysis is to maximize the shape differences between the predefined groups of specimens, relative to the within-group variability (Gittins, 2012). Permutation tests were

performed (10 000 iterations per comparison) on Mahalanobis and Procrustes distances among groups. For each locomotion aspect, the rate of variance given for a canonical variate (CV) corresponds to the variation among group, scaled by the inverse of the within-group variation.

To test the robustness of the locomotion categories, we conducted cross-validation by putting aside one species from the CVA. The grouping of this species was then predicted *a posteriori* based on this analysis. More precisely, we used the relationship between the landmark coordinates and the CV scores in the shape space of the new CVA (without one species) to compute in the new shape space the CV scores of the specimens belonging to this species. One cross-validation test was conducted for each locomotion aspect and each species.

Results

Size

The semicircular canals are smaller for *H. lar carpenteri* compared with the other species (Fig. 2; Table S2). The differences in centroid size are statistically significant among species ($F_{4,60} = 9.433$, $P < 0.0001$), between sexes ($F_{1,51} = 6.446$, $P < 0.05$) and for species–sex interactions ($F_{4,51} = 6.324$, $P < 0.001$). The Tukey HSD test shows significant differences ($P < 0.05$) between *H. lar carpenteri* and every other species. When the specimens of uncertain sex are not taken into account, the differences are also significant between chimpanzees and humans ($P < 0.05$). The differences between males and females are significant only in gorillas ($P < 0.01$) and orangutans ($P < 0.05$). In these species, males are of greater size. The sub-adult chimpanzee (size = 13 638 μm) and orangutan (size = 14 291 μm) are included in the 68.2% confidence interval for the corresponding species, when adults are excluded (Table S2). This is the same for the infant (size = 15 242 μm) and juvenile (sizes = 14 474 and 15 622 μm) gorillas.

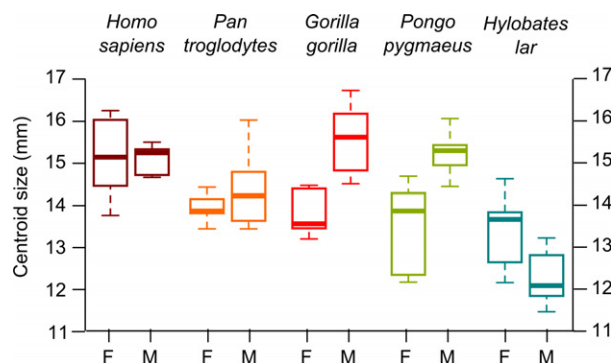


Fig. 2 Centroid size (mm) of the semicircular canals in modern hominoids. For each species, the median, first and third quartiles are represented in the whiskers box. The whiskers correspond to the minimum and maximum values. F, females; M, males.

Static allometry

The first regression score explains 4.8% of total variance. The correlation between log centroid size and shape variables is significant ($P < 0.05$). The quantified shape changes correspond to the anteroposterior lengthening of the ASC and the LSC (Fig. 3). Gibbons, with the lowest regression scores, are clearly separated from Hominidae. The low centroid size of their semicircular canals is associated to an anteriorly projected ASC and a posteriorly projected LSC. With the highest scores, humans are also distinct from the other species, but only in terms of shape, with features opposite to *H. lar carpenteri*. The correlations between regression score and log centroid size are significant for Hominoidea when taken together ($R^2 = 0.35$, $P < 0.0001$). The correlation between shape and size is poor, but statistically significant for Hominidae considered as a whole ($R^2 = 0.120$, $P < 0.01$). However, for each species, the intraspecific correlation between regression score and log centroid size is not significant.

Shape

The regression scores are significantly different between species ($F_{4,60} = 85.59$, $P < 0.0001$). More specifically, gibbons are distinct from hominids ($P < 0.0001$) and humans are discriminated from apes ($P < 0.0001$). There is no sexual dimorphism for the regression score ($P > 0.05$). The sub-adult chimpanzee (regression score = -0.0078) and orangutan (regression score = -0.0249) are included in the 68.2% confidence interval for the adult specimens of the corresponding species (regression scores = -0.0071 ± 0.0180 and -0.0056 ± 0.0263 , respectively). The juvenile gorillas (regression scores = 0.0074 and 0.0166) are included in the 68.2% confidence interval for the adult specimens of this species (regression score = 0.0026 ± 0.0174), but not the infant gorilla (regression score = -0.0175). However, the infant gorilla is included in the global range of regression scores for the adult gorillas (min = -0.0278 ; max = 0.0225).

The PCA was conducted on the regression residuals. The significant PCs are PC1, PC2, PC3 and PC4. They represent 63.4% of the total variance.

The first PC (PC1) accounts for 25.8% of total variance. It quantifies the shape changes that describe the rotation of the whole labyrinth in relation to the LSC in the sagittal plane (Fig. 4a). For the specimens with higher scores, the left bony labyrinth has a clockwise rotation in the lateral view. PC1 also describes the LSC posterolateral projection, which is very developed for lower scores.

The second PC (PC2) accounts for 16.6% of total variance. It quantifies the shape changes that describe the anteroposterior lengthening and torsion of the ASC and LSC (Fig. 4a). The specimens with higher scores show a posteriorly projected LSC and an anteroposteriorly projected ASC.

The third PC (PC3) accounts for 12.2% of total variance. It quantifies the shape changes in the posterior part of the semicircular canal system (Fig. 4b). The specimens with

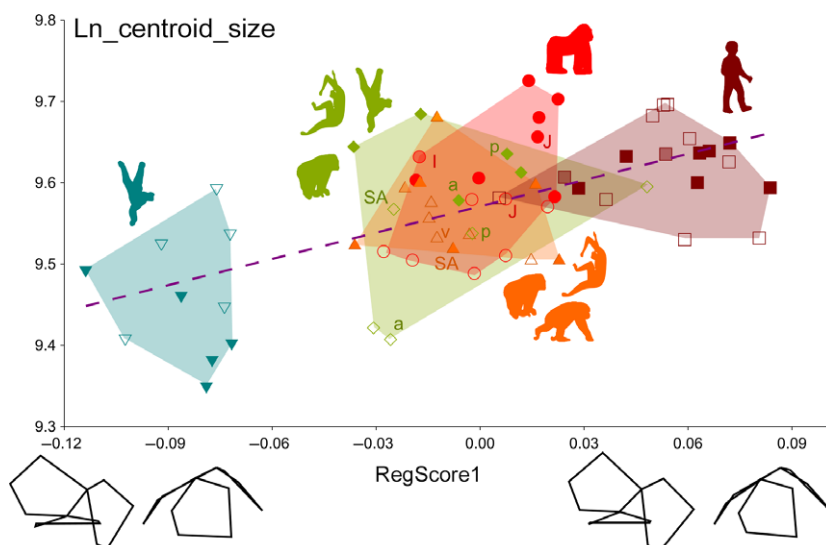


Fig. 3 Natural logarithm of centroid size (μm) vs. regression score 1. The frames represent the extreme morphologies in lateral (left) and superior (right) views. Brown squares: *Homo sapiens*; orange triangles pointing upwards: *Pan troglodytes*; red circles: *Gorilla gorilla*; green diamonds: *Pongo pygmaeus*; blue triangles pointing downwards: *Hylobates lar carpenteri*. The dark filled, empty and light filled symbols represent, respectively, males, females and specimens with uncertain sex determination. The dotted line corresponds to the hominoid major axis regression. a, *P. p. abelii*; p, *P. p. pygmaeus*; v, *P. t. verus*; I, infant; J, juvenile; SA, sub-adult.

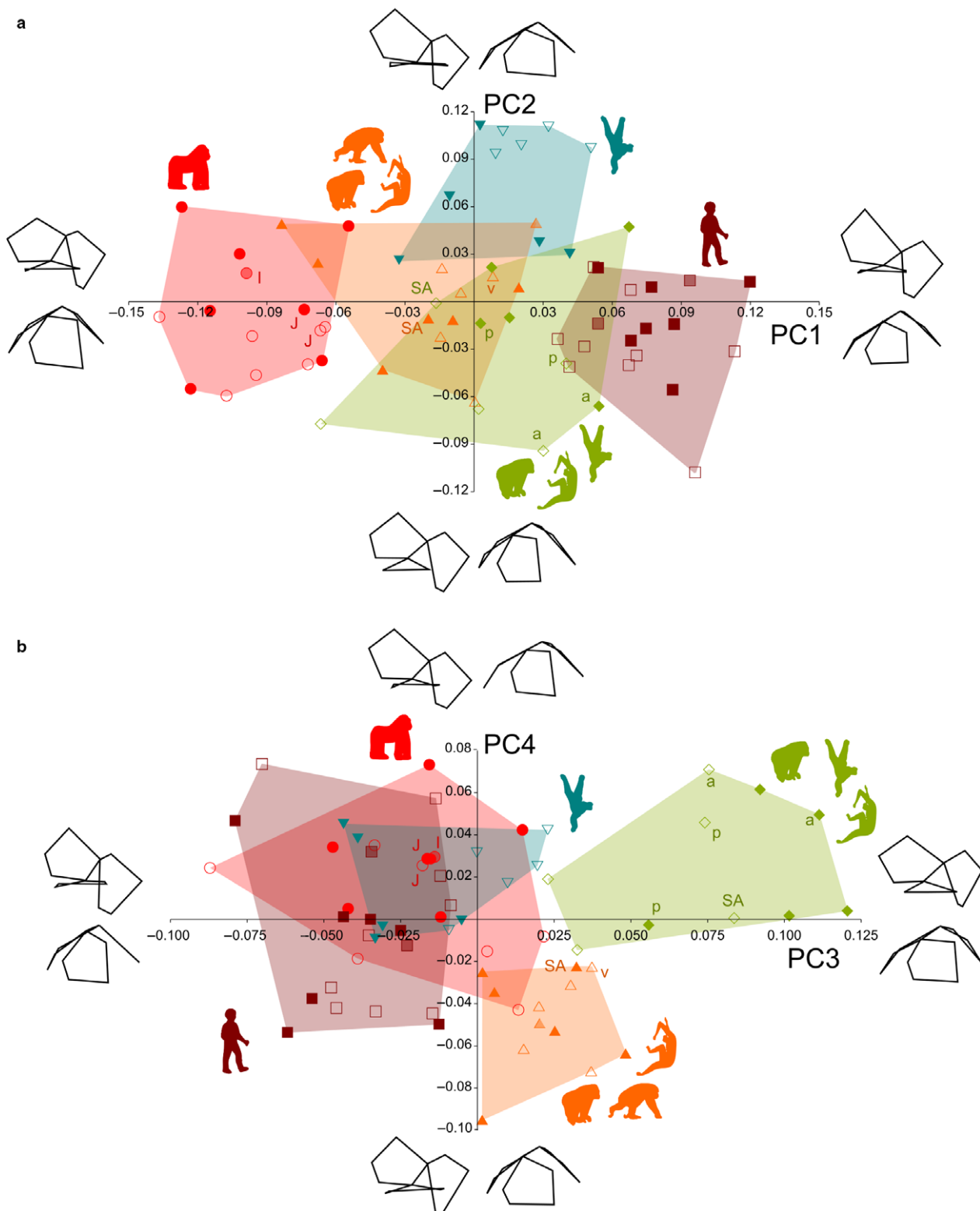


Fig. 4 Comparative hominid morphology. (a) PC2 (16.6% of total variance) vs. PC1 (25.8%). (b) PC4 (8.8%) vs. PC3 (12.2%). The frames represent the extreme morphologies in lateral (top/left) and superior (bottom/right) views. Brown squares: *Homo sapiens*; orange triangles pointing upwards: *Pan troglodytes*; red circles: *Gorilla gorilla*; green diamonds: *Pongo pygmaeus*; blue triangles pointing downwards: *Hylobates lar carpenteri*. The dark filled, empty and light filled symbols represent, respectively, males, females and specimens with uncertain sex determination. a, *P. p. abelii*; p, *P. p. pygmaeus*; v, *P. t. verus*; I, infant; J, juvenile; SA, sub-adult.

higher scores have more twisted LSC and PSC. The posterior part of the LSC is lower. The posterior part of the PSC is superiorly projected and its inferior projection is reduced. The angle between the vertical canals is more open.

The fourth PC (PC4) accounts for 8.8% of total variance. It quantifies the shape changes that describe the PSC posteroinferior projection, the LSC anteroposterior projection and the ASC anterosuperior projection (Fig. 4b). The specimens with higher scores have more lengthened vertical canals but a less projected LSC.

In the shape space of the significant PCs (PC1–4), the differences in the labyrinthine shape are statistically very significant among species (Wilk's $\lambda_{\text{species}} = 0.010$, $F_{4,60} = 38.884$, $P < 0.0001$). There are no significant differences between males and females (Wilk's $\lambda_{\text{sex}} = 0.910$, $F_{1,51} = 1.185$, $P = 0.329$), but sex–species interactions are significant (Wilk's $\lambda_{\text{species} \times \text{sex}} = 0.508$, $F_{4,51} = 2.287$, $P < 0.01$).

Principal component 1 separates humans, with higher scores, from apes, with lower scores. Gorillas, the lowest scores, are also discriminated from the other hominoids. Chimpanzees have lower scores than orangutans and gibbons, but the differences are not statistically significant ($P = 0.113$ and $P = 0.081$, respectively, after the Tukey's HSD test). PC2 discriminates gibbons, with higher scores, from Hominiidae, with lower scores. PC3 and PC4 add supplementary information. PC3 discriminates orangutans, with the highest scores, from chimpanzees, with lower scores. Both of these are different from other species, here the lowest scores. PC4 discriminates chimpanzees, with lower scores, from all species, with higher scores. According to the Tukey's HSD test, all these differences are significant ($P < 0.05$). However, the sexual dimorphism in labyrinth shape is not significant within species.

The most marked differences in semicircular canal shape are associated with PC1 and affect the whole semicircular canal system. In humans, the ASC is superiorly projected, and therefore rounder, and its anterior part is medially projected, not too twisted and roughly orthogonal to the LSC. The LSC is coronally rotated and thus not posterolaterally projected. The insertion of the LSC edge opposite to the ampulla is very high and lateral on the vestibule, which implies a short common crus and an inferiorly located PSC. The superior part of the PSC is rotated coronally. All these features correspond to a

clockwise rotation of the vertical semicircular canals in the sagittal plane, relative to the LSC from a lateral view, along with an anti-clockwise rotation of the superior part of the ASC in the coronal plane, when viewed from the front, and a clockwise rotation of the LSC and the superior part of the PSC in the transverse plane, as seen from above. Gorillas have the opposite morphology: the ASC is twisted, forming an acute angle with the LSC, and not superiorly projected; the LSC is very posterolaterally projected and is inserted less laterally and not as high on the vestibule. Gibbons are characterized by very antero-posteriorly lengthened ASC and LSC, and a large angle between the ASC and PSC due to the anterior projection and torsion of the ASC. For orangutans, the main differences affect the PSC and LSC. The PSC is more twisted, with concavity towards the rear and a flattened posteroinferior part, and the posterior part of the LSC is inferiorly projected. They also have a shortened common crus and an obtuse angle between the ASC and PSC. Chimpanzees have the same features as orangutans for the PSC, but their LSC is flat and anteroposteriorly projected and their ASC is not anterosuperiorly projected.

Phylogenetic signal

In the phylogenetic shape space (Fig. 5), the repartition of the mean morphology of each hominid species is not consistent with the phylogeny. Yet the hylobatid species (*H. lar carpenteri*) is clearly distinct from the hominids along PC2, which is consistent with the phylogeny. According to the permutation test, the phylogenetic signal is not statistically significant either for the Procrustes coordinates ($P = 0.485$) or for the PC scores ($P = 0.791$). It is not significant either for the centroid size ($P = 0.085$).

Locomotion signal

For all aspects of locomotion, groups are clearly separated (Fig. 6), and differences among groups are statistically significant. Indeed, both for Mahalanobis and Procrustes distances, the P -values of the permutation tests are below 0.0001. However, *a posteriori* groupings lead to misclassification for all species regarding substrate use (Fig. S2c) and

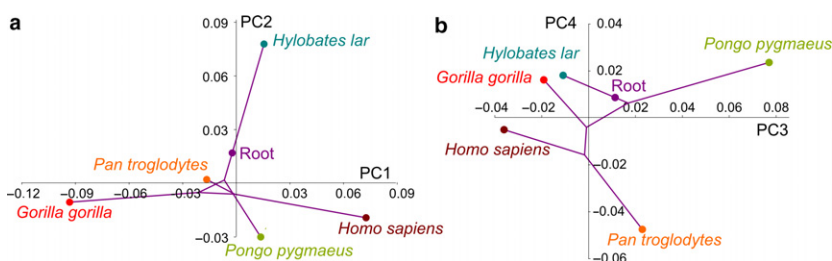


Fig. 5 Phylogenetic shape space. (a) PC2 vs. PC1. (b) PC4 vs. PC3. For each species, the point corresponds to the mean of all individuals. The branch lengths correspond to the phylogenetic distances. The purple circle labeled 'Root' is the root node of the phylogenetic tree.

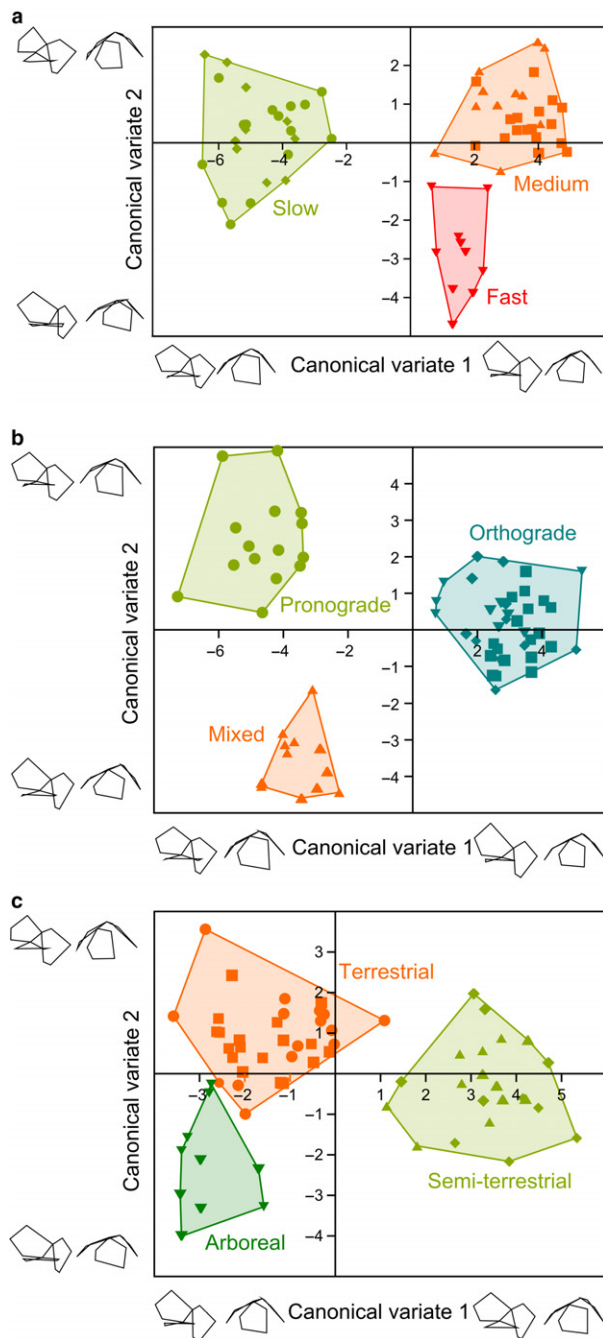


Fig. 6 Canonical variate (CV) scores for each aspect of locomotion. (a) Agility. (b) Posture. (c) Substrate. The frames represent the extreme morphologies in lateral (left) and superior (right) views. The scale factor for CV shape changes is in units of Mahalanobis distance, namely the shape change per unit of within-group shape variation. Squares: *Homo sapiens*; triangles pointing upwards: *Pan troglodytes*; circles: *Gorilla gorilla*; diamonds: *Pongo pygmaeus*; triangles pointing downwards: *Hylobates lar carpenteri*.

for the fast and moderately agile species (Fig. S2a). For postural aspects, *a posteriori* groupings are roughly consistent for all species, except the orthograde orangutans that fall closer to the pronograde gorillas (Fig. S2b).

In the CVA dealing with postural aspects, the first CV represents 76.57% of total variance and discriminates the mainly orthograde species (CV1 > 0) from more pronograde species (CV1 < 0). It quantifies the same shape changes as the first PC of the PCA: the rotation of the whole labyrinth in relation to the LSC in the sagittal plane and the LSC posterolateral projection (Fig. 6b).

The second CV represents 23.43% of total variance, and discriminates the species using both orthograde and pronograde postures (low values) from the species using one main posture (higher values). It quantifies similar shape changes as the fourth PC of the PCA: the lateral projection of the LSC and the posteroinferior projection of the PSC (Fig. 6b).

Discussion

Intraspecific variability

The two specimens attributed to *P. p. abelii* are located at the periphery of the point clouds corresponding to *P. pygmaeus* (Figs 3 and 4). However, they are not very far from the two specimens attributed to *P. p. pygmaeus*, so their size and shape do not seem significantly distinct. The differences between *P. p. pygmaeus* and *P. p. abelii* cannot statistically be tested, as only two specimens are attributed for each subspecies. The specimen attributed to *P. t. verus* is not an outlier when it comes to the point clouds corresponding to *P. troglodytes*, except for the PC3–PC4 shape space, where it is located close to the sub-adult specimen (Figs 3 and 4). Again, the differences cannot be statistically tested.

Five specimens are not adults: one sub-adult chimpanzee, one sub-adult orangutan, one infant and two juvenile gorillas. In mammals, the labyrinth reaches its adult size and shape during fetal development, at about 17–19 weeks of gestation for humans, when the ossification of the otic capsule surrounding the labyrinth is completed (Jeffery & Spoor, 2004; Mejdoubi, 2015; Costeur et al., 2017). The form of the semicircular canals for juvenile and sub-adult apes is within the adult confidence interval. This is consistent with the observations on humans. The infant gorilla is included in the range of adult gorillas for shape, but it does not fall in their confidence interval (Figs 3 and 4). It could be linked to a later development of the labyrinth, in contrast to humans.

In *G. gorilla* and *P. pygmaeus*, males are less arboreal than females and have larger body sizes (Fleagle, 1999). This difference in body size is reflected in the semicircular canal centroid size (Fig. 2; Table S2). However, there is no statistically significant sexual dimorphism in the shape of the semicircular canals. Therefore, the morphology of the semicircular canals within a species reflects its evolutionary history more than the locomotion behavior of one individual.

Allometry

A statistically significant correlation between size and shape is found within hominoids. However, this relationship does not correspond to a continuous shape variation with an increase in size. It looks more like two clouds of points constituting two discrete groups: the small gibbons on one hand, the large hominids on the other hand. Furthermore, both the PC2 and the first regression score discriminate gibbons from hominids and they describe similar shape changes, although these are not as strong for the latter. Rather than being indicative of allometry, these observations lead to speculation as to whether these size/shape relationships reflect a size threshold between small and large hominoids, with size/shape relationships that are specific to each group. However, the relative size of the canals is similar between the small *H. lar carpenteri* and the large *Symphalangus syndactylus* (Spoor & Zonneveld, 1998). An alternative hypothesis is that these shape differences reflect phylogenetic differences between hylobatids and hominids, as the latter are taller than gibbons. A phylogenetic signal is not statistically supported here, but this could be due to the use of only one hylobatid species. The shape of the semicircular canals is not homogenous within hylobatids, but it also looks different from hominids (Spoor & Zonneveld, 1998). It would be interesting to add specimens from other hylobatid species, small and large, to test these differences with 3D geometric morphometrics.

Locomotion

The results of CV analyses tend to support a link between semicircular canal morphology and posture. Indeed, orthograde species are discriminated from more pronograde species along the first CV (Fig. 6b). The closeness of *P. pygmaeus* and *G. gorilla* on the cross-validation tests for orangutans could be linked with their cautious locomotion. Indeed, the shape changes associated to slow and to more pronograde species are very similar (Fig. 6). An alternative explanation is their common use of quadrupedal locomotion on the ground. In both cases, the body stability is higher compared with humans and gibbons.

The LSC of the more pronograde species is posterolaterally projected (Fig. 6b). Because of this projection, the LSC is rotated in the transverse plane backwards in relation to the vertical semicircular canals. Thus, the horizontal and the vertical canals form an acute angle instead of being orthogonal. Consequently, sensitivity is reduced in the roll direction (Muller & Verhagen, 1988, 2002c), which is logical considering that terrestrial quadrupedalism, used by the pronograde species, is a stable locomotor behavior (Schmidt, 2010). Baboons have the same feature as gorillas (Spoor & Zonneveld, 1998) and they are also terrestrial quadrupedalists (Fleagle, 1999), but they have a medium

locomotion agility (Ryan et al. 2012). Therefore, the posterolateral projection of the LSC could be a sign of a quadrupedal locomotion on the ground. Conversely, in the orthograde species, the absence of posterolateral projection of the LSC implies orthogonality between the horizontal and the vertical canals. Therefore, they have similar sensitivities in all rotational directions, which is consistent with the results of Malinzak et al. (2012) for species with faster head rotations.

Moreover, in orthograde species, the vertical semicircular canals are rotated clockwise in the sagittal plane, from the lateral view, in relation to the LSC (Fig. 6b). This leads to more superiorly projected vertical semicircular canals, and thus they are less anteroposteriorly eccentric and relatively larger. The eccentricity of the semicircular canals does not seem to play a role, as there is no link between the height-to-width ratio and locomotion in these species (Spoor & Zonneveld, 1998). However, the large arc size of the ASC and PSC compared with the LSC could be related to locomotion. Indeed, the LSC commands navigation, whereas the vertical semicircular canals control reflex adjustment (Fitzpatrick et al. 2006). So, navigation control might be similar in orthograde and pronograde postures. Conversely, reflex adjustment might be more efficient in the orthograde species. This need for a better reflex adjustment could be explained by the fact that orthograde locomotion is less stable than pronograde locomotion, as the head is higher in relation to the body's center of gravity.

Humans, using exclusively bipedal locomotion, show extreme morphologies among orthograde species (Fig. 6b). Compared with other hominids, they have particularly large vertical semicircular canals and a small LSC. As a result, when it comes to canal arc size relative to body mass, humans follow the non-hominid primate trend for vertical canals and the great apes for the LSC (Spoor & Zonneveld, 1998). Therefore, reflex adjustment might be more efficient in humans, at the level of the agile primates, probably because the body mass is supported by two limbs instead of four and thus it is less stable.

Homo erectus s.l., thought to be a biped, has some of the same features as humans: labyrinth rotation in relation to the LSC in the sagittal plane, LSC posterolateral projection, and semicircular arc sizes in relation to body mass (Spoor et al. 1994). *Homo neanderthalensis* has a labyrinth that is even more rotated in the sagittal plane than modern humans (Hublin et al. 1996; Spoor et al. 2003). In contrast, *Australopithecus africanus* and *Paranthropus robustus*, both thought to be more arboreal, retain great ape features. Late South African australopithecines and early *Homo* have a mosaic of human, great ape and intermediate features (Spoor, 1993). These observations reinforce the hypothesis that these features are signs of bipedalism. In this case, the complete set of 'bipedalism features' would be found in obligatory bipeds only, whereas facultative bipeds would show only a few features.

Limits of the bony labyrinth

In the present study, the hypothesis of relationships between the morphology of the semicircular canals and the mode of locomotion is strengthened. However, some discrepancies remain between the morphological features of the labyrinth and the biophysical models of its operation. For example, the large arc sizes of the ASC and the LSC imply a high sensitivity in fast-moving gibbons, and therefore a risk of overstimulation (Spoor & Zonneveld, 1998). Several factors can explain these discrepancies. Firstly, the functional effects of the duct cross-sectional radii are higher than the arc size (Pfaff et al. 2015). In the case of gibbons, a reduction of the cross-sectional radii of the anterior and lateral ducts could considerably offset the sensitivity increase, while shortening the response time and keeping the flow laminar (Muller, 1999). In relation to hominids, the bony canals are narrower in gibbons, but the corresponding membranous ducts were not observable in this study. A membranous duct is much narrower than the corresponding bony canal, but their relationships in terms of size depend on the species (Curthoys et al. 1977a,b). Therefore, the cross-sectional radii were not taken into account in this study. Secondly, navigation and spatial orientation during locomotion rely on complex multisensorial integration: vestibular afferences with interactions between the semicircular canals and the otolith organs, but also visual and proprioceptive afferences (Kleiber et al. 1990; Allum et al. 1995; Angelaki & Cullen, 2008). Here, only the semicircular canals in the vestibular system were taken into account, because the bony vestibule does not accurately reflect the morphology of the otolith organs. In gibbons, the marked shape differences between the two vertical canals lead to distinct neural impulses, hence a finer interpretation of the head movements by the brain (Muller & Verhagen, 1988). Thirdly, the dimensions of the soft tissues and the mechanical properties such as elasticity, viscosity and porosity of the cupula and the endolymphatic liquid influence the sensitivity and the response time of the vestibular system (Steinhausen, 1933; Van Egmond et al. 1949; Grant & Best, 1986; Rabbitt, 1999). Fourthly, the hair-cell transduction, the synapses and the neural conduction of the signal have much more influence on vestibular sensitivity and response time than the biomechanics of the semicircular canal system (Rabbitt et al. 2004; Highstein et al. 2005; Ifediba et al. 2007). For example, an amplification mechanism of the hair cells increases the sensitivity for a low signal (Rabbitt et al. 2010).

Cranial integration

Compared with great apes, humans are characterized by a basicranial flexure, a more inclined posterior petrosal surface and a more coronal posterior petrosal surface (Aiello & Dean, 1990; Spoor & Zonneveld, 1998;

Lieberman et al. 2000). For other hominoids, the axis of symmetry of the LSC is coronally rotated in humans (Fig. 4a). There is no relationship between the orientation of the LSC axis of symmetry in relation to the labyrinth and the coronal rotation of the petrous pyramids, either in non-human primates (Spoor & Zonneveld, 1998) or during human fetal development (Jeffery & Spoor, 2004). However, during human ontogeny, the coronal rotation of the petrous pyramids is positively correlated to the rotation of the cochlea in relation to the labyrinth and the LSC rotation in the sagittal plane (Jeffery & Spoor, 2004). Therefore, instead of locomotion, the main determinant of the morphology of the labyrinth could be its spatial integration within the base of the skull and, more precisely, inside the petrous pyramids. Among apes, orangutans and gibbons have the most sagittal petrous pyramids (Spoor & Zonneveld, 1998), but they do not have the most sagittal axes of symmetry for the LSC (Fig. 4a). However, they have the most obtuse angles between the ASC and PSC, hence more sagittal vertical canals (Fig. 4). This could be the sign of a different integration pattern between the semicircular canal system and the petrous pyramids, in the transverse plane, in contrast to humans.

In humans, the vertical semicircular canals are also rotated in the sagittal plane in relation to the LSC (Fig. 4a). In primates, a statistically significant correlation exists between the orientation of the LSC in relation to the labyrinth, in the sagittal plane, and the basicranial flexure (Spoor & Zonneveld, 1998). Furthermore, the LSC orientation is correlated with the posterior cranial base orientation in relation to the anterior cranial base. This is independent from the cranial base angle during human fetal development (Jeffery & Spoor, 2004). The flexed cranial base of humans is partly an adaptation to bipedalism (Strait & Ross, 1999; Lieberman et al. 2000). Therefore, in humans, the rotation in the sagittal plane of the ASC and PSC in relation to the LSC is indirectly linked to bipedalism, through the morphology of the cranial base. The interpretation of the rotation of the vertical canals in the sagittal plane is more difficult in the case of other hominoids. Conversely to humans and other hominoids, gorillas have the opposite rotation, but their range of basicranial angles is not different from other great apes (Spoor & Zonneveld, 1998). In contrast, hylobatids have a less flexed cranial base (Spoor & Zonneveld, 1998), but they do not show an extreme 'anti-human rotation' of the vertical canals in relation to the LSC. This discrepancy from the global trend for primates could be explained either by a different integration pattern between the cranial base and the labyrinth, or by a stronger direct functional signal, namely, biomechanical properties directly depending on morphology.

The morphology of the labyrinth also depends on the brain size. In lemurs and lorises, the semicircular canal arc size increases with the brain mass (Malinzak, 2010), and the PSC is more inferiorly positioned in relation to the

LSC (Lebrun et al. 2012). This morphological variation of the labyrinth accompanying brain size, i.e. the ratio of the brain volume to the length of the cranial base, could be a consequence of the petrous pyramid orientation (Lebrun et al. 2012). Indeed, labyrinth shape is correlated to pyramid orientation (Spoor & Zonneveld, 1998; Jeffery & Spoor, 2004), which in turn is correlated to the relative brain size (Spoor, 1997; Spoor & Zonneveld, 1998; Lieberman et al. 2000). However, labyrinth shape changes that accompany an increase in brain mass could also be adaptations for the stabilization of a heavier head. Indeed, bipedal humans have very large brains (Ross & Henneberg, 1995) and a large ASC in comparison to the other hominids (Fig. 4a). This is consistent with features of bipedal non-avian dinosaurs when compared with quadrupedal ones (Georgi et al. 2013).

Evolution

The evolution of posture and locomotion among Hominoidea is subject to several hypotheses. There is a general consensus about the fact that the last common ancestor of the crown hominoids used arboreal orthograde with the ability to abduct the arms above the shoulders (Crompton et al. 2008). The origin of bipedalism, however, is less clear and several hypotheses have been proposed (for a complete review, see Crompton et al. 2008):

- 1 In the first hypothesis, terrestrial bipedalism evolved from a semi-terrestrial ancestor using knuckle-walking and climbing, much like gorillas and chimpanzees (Richmond & Strait, 2000). However, this hypothesis is not very well supported because it implies a transition from orthograde to pronograde, and then back to orthograde, which is not parsimonious. Moreover, the forms of knuckle-walking are different between gorillas and chimpanzees, and no fossil species of the human branch exhibits knuckle-walking features in their hands.
- 2 In the second hypothesis, terrestrial bipedalism directly evolved from arboreal orthograde (Thorpe et al. 2007), which corresponds to crown hominoid locomotion. This hypothesis is supported by the fact that orthograde posture is found not only in suspension, used by all apes, but also in vertical climbing, used by great apes, clambering, used by orangutans, and arboreal bipedalism. Knuckle-walking evolved independently in gorillas and chimpanzees (Thorpe et al. 2007) as a compromise between vertical climbing constraints and body flexion to grasp fallen food on the ground.
- 3 A third hypothesis was proposed after the discovery of *Ardipithecus ramidus*. In this hypothesis, terrestrial bipedalism evolved from a 'generalist palmigrade' ancestor using both terrestrial bipedalism and diverse arboreal locomotor modes including quadrupedalism, which corresponds to stem hominoid locomotion (Lovejoy et al. 2009). It is supported by the hand shape

of *A. ramidus* (Lovejoy et al. 2009) and by the general affinities between an *Australopithecus afarensis* hamate and quadrupedal primates (Daver et al. 2014). However, Crompton et al. (2010) proposed that, given its large body mass, *A. ramidus* used compressive orthograde instead, like crown hominoids.

The bony labyrinth morphology depends on locomotion. The evolution of this morphology can be used to confirm or reject the hypothesis on the evolution of locomotion in hominoids.

Among the catarrhine species observed in this study and in Spoor & Zonneveld (1998), the PSC is not only posteroinferiorly projected for chimpanzees and orangutans. Therefore, this feature probably appeared independently in both species. All catarrhines have a slightly anterosuperiorly projected ASC, except Hylobatidae in which the very pronounced projection could be a derived feature. LSC shape is variable among catarrhines, but it is roughly round except in terrestrial quadrupedalists, such as gorillas and baboons, and bipedalists, the modern humans. Therefore, the following morphology is proposed for the primitive hominoids: a slightly anterosuperiorly projected ASC and round LSC and PSC. This corresponds to *Macaca fascicularis* morphology (Spoor & Zonneveld, 1998), a mainly arboreal quadrupedalist sometimes using leaping, but never suspension (Fleagle, 1999).

Among catarrhines, the ASC is only very anterosuperiorly projected in Hylobatidae (Spoor & Zonneveld, 1998). Therefore, this feature is probably an apomorphy of this family, linked to their suspensory, and less frequently climber behavior. Hominidae do not have this feature, which is against the hypothesis of ancestral arboreal orthograde for bipedalists.

Gorillas and chimpanzees both use knuckle-walking, but they have different labyrinth shapes: whereas the LSC is very posterolaterally projected in gorillas, as it is in baboons, it is rounder in chimpanzees. In contrast, the PSC is round in gorillas and twisted, not posteroinferiorly projected in chimpanzees, as it is in orangutans. This is a supplementary argument for the hypothesis of convergent use of knuckle-walking and against the hypothesis of a semi-terrestrial origin for terrestrial bipedalism.

To summarize, the labyrinthine morphologies found for each extant hominoid species appear to be autapomorphic features, derived from a primitive morphology adapted to an arboreal or semi-terrestrial quadrupedalism similar to the locomotion practiced by macaques. This would be consistent with the third hypothesis for the origin of human terrestrial bipedalism.

Conclusion

In this geometric morphometric study, potential relationships between posture and the labyrinthine morphology are highlighted. More precisely:

- 1 a posterolateral reduction of the LSC and rotation in the sagittal planes of the ASC and PSC in relation to the LSC all speak of orthograde posture, particularly terrestrial bipedalists;
- 2 a posterolateral projection of the LSC indicates stable, pronograde posture as used by terrestrial quadrupedalists.

The morphological features associated with pronograde species are also found in slow-moving species. However, the relationships between labyrinth shape and agility are not supported in this study, unlike studies based on traditional morphometrics (Sporer et al. 2007). The degree of arboreality does not seem reflected by the morphology of the labyrinth.

According to the biophysical models (Jones & Speller, 1963; McVean, 1999; Muller, 1999), each pattern of morphological change described in this study induces variation in sensitivity range and/or preferential orientation. The modifications of the biomechanical properties of the semicircular canal system are roughly consistent with the adaptive hypotheses for each locomotion behavior.

Phylogeny does not seem to significantly influence the morphology of the labyrinth in extant hominoids, at least for the species used in this study, unlike other groups of mammals (Lebrun et al. 2010; Grohé et al. 2015; Ekdale, 2016). However, the morphology of the labyrinth could be influenced by cranial morphology. Previous studies have linked the rotation of the LSC in the sagittal plane to the posterior cranial base orientation in humans (Jeffery & Spoor, 2004). The rotation of the labyrinth in relation to the cochlea, observed in humans and gorillas in opposite directions, is also linked to petrous pyramid orientation in relation to the midsagittal plane (Jeffery & Spoor, 2004). The opening of the angle between ASC and PSC, observed in Asian apes, is most likely to be a consequence of the same parameter. This cranial integration is not incompatible with the relationships between the morphology of the bony labyrinth and locomotion, as the shape of the base of the skull is partly correlated with locomotion.

To further investigate the relationship between the bony labyrinth and the cranium, it could be interesting to study the ontogeny of gorillas, as they have the opposite morphology to humans. A comparative study of human and chimpanzee developments before and after birth could also provide more detail on the relationship between the cranial base and the labyrinth, as the basicranium flexes for the former while it retroflexes for the latter (Lieberman & McCarthy, 1999). Another interesting issue is the evolution of the labyrinth of Hominidae in contrast to other anthropoids. It could be addressed by a combination of anatomical, genetic and ontogenetic comparisons.

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Authors' contributions

A.L.M., M.B. and P.V. designed the study. A.L.M. and P.S. scanned the skulls. A.L.M. segmented the bony labyrinths and performed the analyses. A.L.M., M.B. and P.V. wrote the paper together.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

File S1. Consensus tree for the hominoids.

Fig. S2. Cross-validation canonical variate analyses. Each plot corresponds to the CV shape space computed without the species whose name is ahead. The specimens belonging to this species (in brown) are a posteriori positioned. (A) Agility; (B) Posture; (C) Substrate.

Table S1. Detailed sample.

Table S2. Centroid size of the semicircular canals.